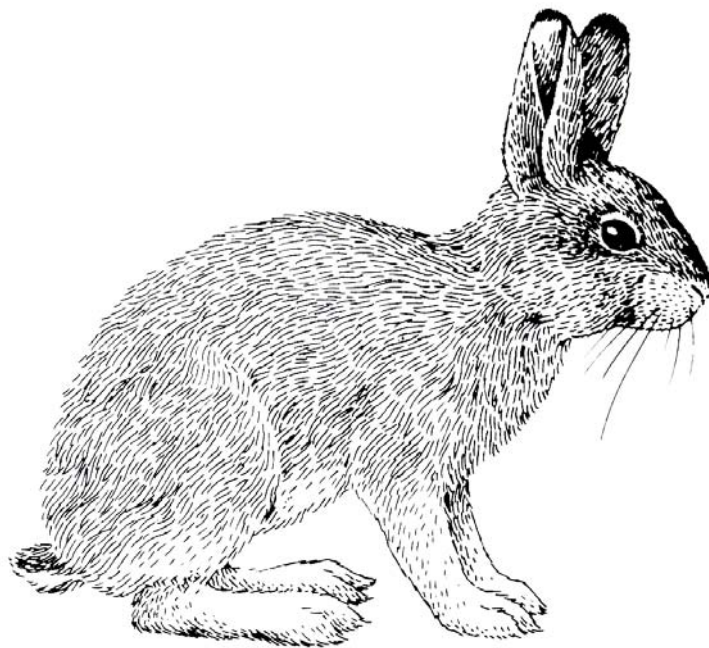


**California Wildlife Habitat Relationships Program
California Department of Fish and Game**

**HABITAT SUITABILITY MODELS FOR USE WITH ARC/INFO:
SNOWSHOE HARE**



CWHR Technical Report No. 20
Sacramento, CA
June 1995

June 1995

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SNOWSHOE HARE

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Suggested Citation: Timossi, I. C., E. L. Woodard, and R. H. Barrett. 1995. Habitat suitability models for use with ARC/INFO: Snowshoe hare. Calif. Dept. of Fish and Game, CWHR Program, Sacramento, CA.
CWHR Tech. Report No. 20. 32 pp.

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SNOWSHOE HARE (*Lepus americanus*)

HABITAT USE INFORMATION

General

The snowshoe hare (*Lepus americanus*) is indigenous to boreal forests throughout North America (Dolbeer and Clark 1975). In California, they are uncommon residents at upper elevations in the Cascade and Warner mountains and in the Sierra Nevada range (Zeiner et al. 1990). Snowshoe hares consume herbaceous vegetation during the growing season and change to a woody diet in the fall and winter (Baker et al. 1921; Dodds 1960). Young forests with abundant understory that provide food and cover are preferred habitat (Grange 1932). In California, they are primarily found in montane riparian habitats with thickets of alders (*Alnus* spp.) and willow (*Salix* spp.) and in stands of young conifers interspersed with chaparral. Habitats used by snowshoe hares include early seral stages of mixed-conifer, subalpine conifer, red fir (*Abies magnifica*), Jeffrey pine (*Pinus jeffreyi*), lodgepole pine (*P. contorta* var. *murrayana*), and aspen (*Populus tremuloides*) (Orr 1940; Ingles 1965). Snowshoe hares exhibit approximate 10-year cycles of abundance and scarcity throughout much of their range. These cycles have been attributed to hare-food interactions (Vowles 1972; Keith and Windberg 1978; Pease et al. 1979; Byrant 1981a; Keith 1983; Keith et al. 1984) and hare-food-predator interactions (Keith 1974; Wolff 1980, 1981). Snowshoe hare population cycles have not been documented in California.

Food

During spring and summer, snowshoe hares feed on a wide variety of herbaceous vegetation, including grasses (Poaceae), legumes (Leguminosae) (Brooks 1955), sedges (*Carex* spp.), ferns (Polypodiaceae) (Dodds 1960), and the leaves of deciduous trees (Wolff 1978). Dead grass, small twigs, buds, bark, conifer needles, lichens, and mosses (Lycopodiaceae) make up their fall and winter diet (Severaid 1942). In Alaska, the general trend in hare seasonal food habits was from browse and black spruce (*Picea mariana*) bark and needles in winter to leaves and other herbaceous material in the spring and summer (Wolff 1978). The quantity of spruce and woody browse in the diet decreased from 82% in winter to 25% in May as the intake of herbs increased from 2% to 49% over the same time interval (Wolff 1978).

The composition of snowshoe hare diets may be influenced by the frequency, density, nutritive value, and palatability of the available plant species (Wolff 1978). Telfer (1972) noted a high degree of adaptability by snowshoe hares to the browse species available with hares utilizing 96% of the species present in a sugar maple-yellow birch-balsam fir (*Acer saccharum*-*Betula alleghaniensis*-*Abies balsamea*) forest and 97% of the species present in a red spruce-hemlock-white pine (*Picea rubens*-*Tsuga canadensis*-*Pinus strobus*) forest. Foraging hares can exhibit decided preferences for specific browse species (Criddle 1938; deVos 1964; Hansen and Flinders 1969). In Eastern Canada, deVos (1964) observed that whenever conifers were available in smaller quantities than deciduous species, the former were browsed more heavily. Conversely, Telfer (1972) found that deciduous species were more heavily browsed than the more abundant evergreen species. Preferential feeding by snowshoe hares can change plant species composition

and affect the future availability of plants (Cook and Robeson 1945; deVos 1964; Bryant 1987).

Snowshoe hares selectively browse on certain parts of a plant. Vowles (1972) noted that small twigs were the preferred food of hares in Alberta, and rough bark and stem wood were referred to as "starvation foods". There is a direct correlation between woody stem diameter and nutritional quality (Grigal and Moody 1980; Wolff 1980). Pease et al. (1979) found that when captive hares in Alberta were supplied with adequate quantities of browse, they selected for terminal twigs 4 mm (0.2 in) in diameter. Keith (1974) believed browse 3 mm (0.1 in) was essential for snowshoe hare survival. Wolff (1980) stated that snowshoe hares normally consume browse 3 mm (0.1 in) in diameter and that 3 mm (0.1 in) diameter twigs contained more nutrients than did twigs of greater diameter. Wolff (1980) suggested that the consumption of twigs with diameters > 3 mm was a sign that the hares were exceeding the habitat's carrying capacity and consequently were feeding on low quality forage. Grigal and Moody (1980) found that in Minnesota the maximum stem diameter at point of browsing (dpb) was 1 cm (0.4 in). Wolff (1980) found that hares at high density in Alaska ate browse that exceeded 1 cm (0.4 in) dpb. A dpb of 1.5 cm (0.6 in) was the maximum believed to be clipped by hares in Alberta (Vowles 1972; Pease et al. 1979).

The supply of high quality winter browse is one of the most crucial factors affecting snowshoe hare survival in northern areas (Walski and Mautz 1977). Vowles (1972) and Pease et al. (1979) determined that only part of the total standing biomass of woody browse is sufficiently digestible or nutritious to sustain snowshoe hares in Alberta. They estimated that 3,000 g (105 oz) wet weight of browse 1.5 cm (0.6 in) in diameter must be available to a hare each day. A hare then can select 300 g (11 oz) of essential food in the form of choice terminal twigs, buds, and bark.

The palatability of browse has been shown to be directly proportional to its nutritive quality (Bryant 1981b; Bryant and Wieland 1985). Bryant (1981a) suggested that high populations of snowshoe hares that deplete the supply of preferred foods are forced to feed on low-preference browse species. This initiates a crash in the population even though the total supply of small diameter twigs has not yet been exhausted. Snowshoe hares in Alaska moved when they had increased in numbers and had depleted their food supply (Wolff 1980). Vowles (1972) noted an inverse relationship between the abundance of browse and the number of snowshoe hares in Alberta. Browse abundance declined after several years of browsing by high populations of hares. When hare populations declined, browse abundance increased correspondingly.

Various species and different parts of plants can produce resins that are unpalatable to hares (Bryant 1981a). Some plant species found to be unpalatable to snowshoe hares are listed in Table 1. In the Northwest Territories, black spruce became more palatable to snowshoe hares after fire had denatured the resinous defense chemicals produced by this species (Stephenson 1985).

Table 1. Plant species unpalatable to snowshoe hares.

Species	Location	Source
Balsam fir (<i>Abies balsamea</i>) American linden (<i>Tilia americana</i>)	Michigan	Bookhout (1965a)

Black cherry (<i>Prunus serotina</i>)		
Red-osier dogwood (<i>Cornus stolonifera</i>)		
Viburnum (<i>Viburnum cassinoides</i>)		
Winterberry holly (<i>Ilex verticillata</i>)		
Black ash (<i>Fraxinus nigra</i>)		
European red elder berry (<i>Sambucus pubens</i>)		
Black spruce (<i>Picea mariana</i>)	Alberta	Keith et al. (1984)
Labrador tea (<i>Ledum groenlandicum</i>)		
Viburnum (<i>V. edule</i>)		
Honeysuckle (<i>Lonicera glaucescens</i> , <i>L. involucrata</i>)		
Snowberry (<i>Symphoricarpos occidentalis</i>)		
Green alder (<i>Alnus crispa</i>)	Alberta	Cary (pers. comm.)

Water

Snowshoe hares are believed to satisfy their water needs from dew and succulent plants in the summer and by eating snow in the winter (Hansen and Flinders 1969).

Cover

Habitat quality for snowshoe hares is determined primarily by the presence of adequate understory cover (Bider 1961; Conroy et al. 1979; Wolff 1980; Buehler and Keith 1982; Wolfeet al. 1982; Litvaitis et al. 1985; Litvaitis 1990; Ferron and Ouellet 1992). Understory species composition may also influence habitat use (Bider 1961; Tompkins and Woehr 1979; O'Donoghue 1983). Habitat requirements may also vary with activity (Bider 1961; Conroy et al. 1979; Belovsky 1984). It has been suggested that cover availability is a more significant habitat variable than the availability of food (Bookhout 1965a, 1965b; Buehler and Keith 1982). In addition to supplying winter browse, low brushy coniferous and deciduous vegetation serves as protection from predators and as shelter from inclement weather (Buehler and Keith 1982).

Habitats dominated by coniferous vegetation are preferred. In Nova Scotia, snowshoe hare pellet densities recorded in coniferous habitats were twice as high as those recorded in deciduous cover (Orr and Dodds 1982). Coniferous lowland forests and conifer plantations were classified as optimum habitat in Wisconsin (Buehler and Keith 1982). Swamp conifer was the most favorable habitat in northern Michigan (Bookhout 1965a,b), and young softwood swamp and fir (*Abies* spp.) thickets were preferred in Maine (Severaid 1942). Snowshoe hares in southern Ontario were chiefly found in poorly drained or swampy areas in which there was heavy coniferous cover (deVos 1962). Coniferous understories contained the greatest number of hares in Montana (Adams 1959), New York (Brocke 1975), and in Alaska (Wolff 1980).

Deciduous cover also can be an important component of the snowshoe hares' habitat. Although in the Virginia and West Virginia, snowshoe hares are mainly restricted to areas of red spruce, although second growth forests of birch-beech-maple (*Betula-Fagus-Acer*) were found to harbor "fair" populations (Brooks 1955). This was most often true when the forest had a rhododendron (*Rhododendron maximum*) or heavy evergreen heath understory. Alder and willow thickets have

been described as good winter cover both in Wisconsin (Bailey 1946) and Alaska (Wolff 1980). Tompkins and Woehr (1979) reported that immature hardwood habitat, which provided abundant winter browse and cover, was preferred in New York. They concluded that snowshoe hares may be best adapted to this habitat type, and that they may use small conifer stands when immature hardwood stands are scarce. In Utah, aspen stands with dense understories were believed to constitute marginal-to-good snowshoe hare habitat (Wolfe et al. 1982).

Apparently, a wide variety of forest types can be utilized if adequate cover is available. Pietz and Tester (1983) believed that, regardless of the species composition of the stand, cover quality is the crucial factor defining habitat preference. Grange (1932) stated that snowshoe hares can occupy fairly mature woodlands if beaver (*Castor canadensis*) are present since hares make use of cuttings left from beaver foraging activities. Brush piles were heavily used in New York and may have been important to hare survival where conifers were sparse or absent (Richmond and Chien 1976). Old burns containing dense brush and dead and down material can also be extensively used as cover (Grange 1932). Snowshoe hares often are most abundant in sapling and pole-stage forest stands (Brooks 1955; Bookhout 1965a; Richmond and Chien 1976).

The relationship between the amount of cover and snowshoe hare abundance has been investigated by several researchers. Adams (1959) subjectively evaluated cover conditions in Montana. He found that, based on mean pellet densities, snowshoe hares preferred "heavy" cover (dense stands of early pole-size Douglas-fir [*Pseudotsuga menziesii*] with abundant ground litter of dead saplings and tree limbs) to "light" cover (open stands of Ponderosa pine [*Pinus ponderosa*] with no shrub understory). In New York, lateral visibilities as measured by a density board in "base cover" varied from 2% (98% obstruction) at 5 m (17 ft) to 0% (100% obstruction) at 20 m (66 ft) (Brocke 1975). In contrast, lateral visibilities in "travel cover" ranged from 15% at 5 m (17 ft) to 3% at 20 m (66 ft). Brocke (1975) suggested that lateral visibility is the single most important stimulus in selecting cover to avoid predation. Wolfe et al. (1982) determined that areas with horizontal vegetation densities of 40% (60% visibility) to 100% (0% visibility), as read from a profile board at a distance of 15 m (50 ft), can be adequate snowshoe hare winter habitat in Utah. In eastern Quebec, lateral foliage densities as measured by profile board at 15 m (50 ft) averaged 90% and 84% respectively in areas used by foraging and resting hares compared to 59% in areas receiving low utilization by hares (Ferron and Ouellet 1992). In Maine, during the winter, snowshoe hares preferred areas where visual obstruction exceeded 60% (Litvaitis et al. 1985). When the density of the understory was sufficient, softwood overstories were preferred over coniferous overstories (Litvaitis et al. 1985). In a study of snowshoe hare use of conifer plantations, Parker (1986) found that the hares preferred jack pine (*Pinus banksiana*) stands when the plantations were approximately eight years old, but this preference switched to black spruce (*Picea mariana*) as the stands aged. This study indicated that conifer cover 1-3 m (3-10 ft) above the ground was the most important factor controlling snowshoe hare distributions in conifer plantations.

Vertical foliage density is thought to be another important factor in habitat preference (Wolff 1980). Brocke (1975) concluded that tree height was the most important factor determining base cover. Heavy cover 3 m (10 ft) above the surface provides concealment from avian predators, whereas heavy cover < 1 m (3 ft) above the ground provides concealment from terrestrial

predators (Wolff 1980). Pietz and Tester (1983) noted that in Minnesota an increase in the number of snowshoe hare pellets coincided with an increase in shrub cover > 1 m (3 ft) in height.

The abundance of forage generally varies inversely with the density of tree cover as tree shading inhibits the growth of herbaceous and shrubby food plants (Adams 1959). In Nova Scotia, Orr and Dodds (1982) found a trend for reduced snowshoe hare densities in areas characterized by canopy closures in excess of 60% and by trees greater than 12 m (40 ft) in height. Similarly, Richmond and Chien (1976) noted that in New York snowshoe hares avoided red pine (*P. resinosa*) plantations where most of the lower limbs were either dead or missing, and a dense canopy inhibited the growth of understory vegetation. In Utah, however, the removal of aspen overstory in areas of dense understory resulted in a marked decrease in hare use suggesting that overstory also is an important habitat component (Wolfe et al. 1982). In Michigan, cover provided by the understory was more important in defining snowshoe hare use than was the cover provided by the overstory (Bookhout 1965a).

Reproduction

Criddle (1938) described a snowshoe hare nest as a shallow depression in dead leaves beneath a leaning tree or among scrub, while Cory (1912) described the nest as being composed of a mass of grass covered with fur and concealed under a bush or weeds. However, other workers contend that no nest is constructed (Adams 1959; L.B. Keith, letter dated January 1985). Adams (1959) found a small pile of evergreen saplings that was used as a "nursery".

Young snowshoe hares leave the location of birth within a few days and scatter into the surrounding undergrowth (Criddle 1938; Rongstad and Tester 1971). Young snowshoe hares in Minnesota spent the days in separate hiding places and came together once a night to nurse (Rongstad and Tester 1971). Severaid (1942) found that captive snowshoe hares began to feed on vegetation at 10-12 days of age and suggested that wild hares become independent at two weeks of age.

In spite of adequate spring herbaceous growth, a shortage of winter browse can affect the reproductive performance of females throughout the summer. The deleterious effects suffered by the females affects in turn the survival of juveniles in the summer (Vowles 1972; Vaughan and Keith 1981). Vowles (1972) also suggested that light-weight juvenile hares suffer high mortality during the transition period between a summer herbaceous diet and a fall diet of browse.

Interspersion and Composition

Snowshoe hares travel via runways that are used year-round (Grange 1932; Criddle 1938). Runways are used when crossing open areas from one stand of dense vegetation to another (O'Farrell 1965) and allow quick escape from predators through thick underbrush (Criddle 1938). Snowshoe hares also are known to swim back and forth across rivers (Criddle 1938; Hunt 1950). Travel through open areas usually occurs only at night (Aldous 1937; Bider 1961; Brocke 1975).

Snowshoe hares occupy home ranges that may overlap considerably. Most authorities believe

snowshoe hares have an active core area of 2-3 ha (5-8 ac), and that 8-10 ha (20-25 ac) are the limits of home range (Wolff 1980). In Wisconsin, home ranges of hares occupying two large (23 ha [58 ac]) and five small (7 ha [18 ac]) habitat patches were similar in size, averaging 2.9 ha (7.3 ac) and 3.0 ha (7.5 ac), respectively (Keith et al. 1993). Maximum hare densities averaged 1.6/ha (2.5 ac) and were unrelated to habitat patch size. In eastern Quebec, mean home range size for males (2.8 ha [7 ac]) was significantly larger than for females (1.4 ha [4 ac]) (Ferron and Ouellet 1992). Females occupied areas averaging 1.1 ha (3 ac) each during feeding and resting periods, while males utilized areas averaging 2.4 ha (6 ac) and 1.9 ha (5 ac), respectively (Ferron and Ouellet 1992). However, home ranges probably vary with the cover type (Severaid 1942).

Habitat interspersation is an important factor determining snowshoe hare density and activity. Tompkins and Woehr (1979) reported that in New York hare density in an area of numerous cover types was nearly twice that of an adjacent area with fewer cover types. In a patchy environment which provides dense cover in winter and more open foraging areas in summer, snowshoe hares are able to shift seasonally in response to changes in diet and to take advantage of changing environmental conditions (Wolff 1980). In Montana, however, Adams (1959) found that as food growing in areas of dense cover was used up, hares were attracted away from cover to feed and thus became more vulnerable to predation. He concluded that snowshoe hare distribution was a result of adjustments among the spatial relationships of food, cover, and predators.

Habitat selection can be influenced by the season of the year. Although forage was plentiful in summer, Bider (1961) found that in Quebec snowshoe hare movements and home ranges during the rest of the year were influenced by the availability of certain plant species. In Alaska, however, Wolff (1980) found that because summer foods did not exist in dense winter refuge areas, snowshoe hares moved to more open areas in the summer. He also suggested that seasonal movements were in response to forage preferences. Pietz and Tester (1983) noted that snowshoe hares in Minnesota used areas of deciduous vegetation more often during snow-free periods because of a dietary shift.

Snowshoe hares occasionally leave areas of cover to forage. Vowles (1972) noted that in Alberta hares from areas with high population density crossed large fields to feed at grainaries and entered farmyards to feed on hay bales. However, open areas are apparently used most often when there is nearby cover. Wolff (1980) in Alaska and Wolfe et al. (1982) in Utah found that snowshoe hares moved to more open areas to forage during the summer growing season if adequate cover was near by. Snowshoe hares in Newfoundland entered open areas in winter by traversing alder beds or broken stands of conifers (Dodds 1960). Feeding is often concentrated along the edges of cover (Cook and Robeson 1945; Richmond and Chien 1976; Conroy et al. 1979).

Cover continuity is an important habitat factor. Brocke (1975) found that in New York small, discontinuous patches of forest were used as travel cover but not as base cover. In Utah, hares concentrated their activities on small islands of prime habitat created by the clumped distribution of young fir trees (Wolfe et al. 1982). The use of a mature forest is often dependent primarily upon the interspersation of openings (Dodds 1960; Grange 1965). Brocke (1975) suggested that the maximum width of continuous base and travel cover tracts should not exceed 200 m (660 ft)

unless interspersed with openings of browse. Conroy et al. (1979) believed that cover should not exceed a distance of 200-400 m (660-1,320 ft) from cutover areas.

Adequate interspersed cover is often most critical during the winter. Conroy et al. (1979) determined that in Michigan white cedar (*Thuja occidentalis*)-fir cover acted as "reservoirs" where snowshoe hare populations lived during the winter. Baker et al. (1921) and Criddle (1938) noted that snowshoe hares in Utah and Manitoba scattered in the spring and summer but congregated in thickets after heavy winter snows. Snowshoe hares in Alaska distributed themselves evenly throughout all suitable habitats during summer (Wolff 1980). In winter, they moved to an area that provided 75% vertical foliage density (25% visibility) at all levels up to 4 m (13 ft). Grange (1965) noted that snowshoe hares in Minnesota were forced to move when deep snows covered pine trees that were 1 m (3 ft) high. Snowshoe hares in Quebec were more active in summer due to the cover provided by the seasonal increase in canopy density (Bider 1961). In the fall, snowshoe hare tracks were found crossing a large plain in Manitoba when hares were leaving outlying bushes and the less dense parts of large woods for more dense areas (Criddle 1938).

Population pressures also can affect the availability of adequate cover. Throughout its geographic range, the snowshoe hare utilizes sites providing dense understory cover at all seasons. More open cover types are occupied temporarily only during periods of high hare density (Windberg and Keith 1978; Wolff 1980). Dispersal movements have been observed when young snowshoe hares augment populations in large numbers (Adams 1959; Dolbeer 1972). In the western United States, snowshoe hare habitat is often discontinuous and dispersing juvenile hares may be forced to move into less favorable, more open habitats (Dolbeer 1972; Dolbeer and Clark 1975). In Wisconsin, rates of hare movement and losses to predation were strongly associated (Sievert and Keith 1985). Predation was higher among dispersers than among residents and for dispersers that moved most. Predation also increased if movement was increased as the result of sparse understory cover, if resident hare populations were present, and probably if the habitat was fragmented (Sievert and Keith 1985). During population increases in Alaska, snowshoe hares disperse to less favorable habitat (Wolff 1981). When a population declines, hares avoid local extinction by seeking refuge in dense cover (Keith 1966; Wolff 1980). Wolff (1980) believed that the magnitude and frequency of cycles can be controlled in part by the size and number of such areas of cover.

Snowshoe hares can be affected by barriers to normal movement. In Michigan, the movements of snowshoe hares appeared to be inhibited by areas of sparse woody cover (Conroy et al. 1979). Brocke (1975) found that hares in New York crossed a clearing 70 m (230 ft) in width by using a narrow neck dominated by sparse conifer cover. He also found a two-lane paved highway to be a major barrier to movements.

Special Considerations

Snowshoe hare populations exhibit eight to 11-year cycles in Alaska (Wolff 1980) and all Canadian provinces except the Maritimes (Keith 1963). Populations in the northeastern (Cook and Robeson 1945) and western (Howell 1923) United States do not

exhibit extreme fluctuations in numbers. The magnitude of cycles increases northward over the snowshoe hares' range (Adams 1959).

Predators exhibit a well-defined functional and numerical response to changes in snowshoe hare abundance (Keith et al. 1977). Major predators in the North include the lynx (*Lynx canadensis*), northern goshawk (*Accipiter gentilis*), great horned owl (*Bubo virginianus*), red fox (*Vulpes fulva*), red-tailed hawk (*Buteo jamaicensis*), and pine marten (*Martes americana*). The red fox, coyote (*Canis latrans*), and bobcat (*Lynx rufus*) are important southern predators (Wolff 1980). In Wisconsin, predation by coyotes was responsible for 96% of natural deaths among radio-collared hares (Keith et al. 1993). Dogs (O'Farrell 1965) and house cats (Severaid 1942) can be important predators in settled areas.

Lack of adequate cover (Cook and Robeson 1945; Bookhout 1965a, Brocke 1975), scarcity of winter food (deVos 1964; Vowles 1972; Walski and Mautz 1977), and severe winter weather (Meslow and Keith 1971; Vowles 1972) may limit populations of snowshoe hares. Conroy et al. (1979) believed that winter represented the critical season for snowshoe hares in Michigan.

Snowshoe hares can experience competition from other animals. Dodds (1960) believed that overgrazing by domestic sheep in Newfoundland caused summer food scarcity for the hares and limited their populations. Moose (*Alces alces*) (Dodds 1960) and white-tailed deer (*Odocoileus virginianus*) (Bookhout 1965a,b) can reduce the amount of food and cover available to snowshoe hares. Cottontail rabbits (*Sylvilagus* spp.) and snowshoe hares can exclude one another in areas of habitat suitable to both species (Buehler and Keith 1982).

Modifications of habitat, through drainage and deforestation can eliminate snowshoe hares from a region (deVos 1962; Windberg and Keith 1978). Large numbers of snowshoe hares can be a serious decimating factor to natural regeneration in forest stands and in tree plantations (Baker et al. 1921). Barking and browsing damage can kill, deform, and reduce the vigor of trees and shrubs (deVos 1964). Snowshoe hares prefer the increased food and cover associated with overstocked stands (Sullivan and Sullivan 1982, 1983). In a stand of young sapling and pole-size lodgepole pine in British Columbia, these authors found maximum hare damage with a stocking rate of about 35,000 stems/ha (2.5 ac), and minimum damage at 5,000 to 10,000 stems/ha (2.5 ac). To minimize snowshoe hare damage, Cox (1938) recommended against heavy plantings that would provide good cover while trees are still small and low enough to be browsed. Bailey (1946) and Sullivan and Sullivan (1982) made three recommendations: (1) plant during periods of low snowshoe hare abundance; (2) thin the stands during a period of predicted damage; and (3) provide fallen pine foliage and slash as alternate food sources.

Browsing by snowshoe hares also can be useful in accelerating tree growth (Cox 1938; Cook and Robeson 1945) and in thinning stands (Roe and Stoeckeler 1950). Snowshoe hare habitat can be enhanced both by clearcutting (Conroy et al. 1979; Tompkins and Woehr 1979; Wolfe et al. 1982) and prescribed burning (Tompkins and Woehr 1979; Wolff 1980). Grange (1965) stated that fire and other disturbances cause hares to survive in small numbers in mature forests. Buehler and Keith (1982) believed that suitable snowshoe hare habitat increases in the absence of

extensive fires and logging. Adams (1959) recommended light thinning of densely forested areas to allow the growth of forage plants and the planting of clumps of coniferous cover in areas with inadequate cover. Conroy et al. (1979) believed that cutover areas can be enhanced for snowshoe hares by leaving slash on the site.

HABITAT SUITABILITY INDEX (HSI) MODEL

Model Applicability

Geographic area.

The California Wildlife Habitat Relationships (CWHR) Database System (Airola 1988; Mayer and Laudenslayer 1988; Zeiner et al. 1990) contains habitat ratings for each habitat type predicted to be occupied by snowshoe hare.

Season.

This model is designed to predict the suitability of habitat for snowshoe hare throughout the year. Model predictions, however, may be more accurate for breeding habitat.

Cover types.

This model can be used anywhere in California for which an ARC/INFO map of CWHR habitat types exists. The CWHR System contains suitability ratings for reproduction, cover, and feeding for all habitats snowshoe hare are predicted to occupy. These ratings can be used in conjunction with the ARC/INFO map to model wildlife habitat suitability.

Minimum habitat area.

Minimum habitat area is defined as the minimum amount of contiguous habitat required before a species will occupy an area. Specific information on minimum areas required for snowshoe hares was not found in the literature. This model assumes two home ranges is the minimum area required to support a snowshoe hare population.

Verification level.

The spatial model presented here has not been verified in the field. The CWHR suitability values used are based on a combination of literature searches and expert opinion. We strongly encourage field testing of both the CWHR database and this spatial model.

Model Description

Overview.

This model uses CWHR habitat type as the main factor determining suitability of an area for this species. A CWHR habitat type map must be constructed in ARC/INFO GRID format as a basis for the model.

The following sections document the logic and assumptions used to interpret habitat suitability.

Cover component.

A CWHR habitat map must be constructed. The mapped data (coverage) must be in ARC/INFO GRID format. A grid is a GIS coverage composed of a matrix of information. When the grid coverage is created, the size of the grid cell should be determined based on the resolution of the habitat data and the home range size of the species with the smallest home range in the study. You must be able to map the home range of the smallest species with reasonable accuracy. However, if the cell size becomes too small, data processing time can increase considerably. We recommend a grid cell size of 30 m (98 ft). Each grid cell can be assigned attributes. The initial map must have an attribute identifying the CWHR habitat type of each grid cell. A CWHR suitability value is assigned to each grid cell in the coverage based on its habitat type. Each CWHR habitat is rated as high, medium, low or of no value for each of three life requisites: reproduction; feeding; and cover. The geometric mean value of the three suitability values was used to determine the base value of the cell for this analysis.

Distance to water.

No water requirement was found for this species.

Species' distribution.

The study area must be manually compared to the range maps in the CWHR Species Notes (Zeiner et al. 1990) to ensure that it is within the species' range. All grid cells outside the species' range have a suitability of zero.

Spatial analysis.

Ideally, a spatial model of distribution should operate on coverages containing habitat element information of primary importance to a species. For example, in the case of woodpeckers, the size and density of snags as well as the vegetation type would be of great importance. For many small rodents, the amount and size of dead and down woody material would be important. Unfortunately, the large cost involved in collecting microhabitat (habitat element) information and keeping it current makes it likely that geographic information system (GIS) coverages showing

such information will be unavailable for extensive areas into the foreseeable future.

The model described here makes use of readily available information such as CWHR habitat type, elevation, slope, aspect, roads, rivers, streams and lakes. The goal of the model is to eliminate areas that are unlikely to be utilized by the species and lessen the value of marginally suitable areas. It does not attempt to address all the microhabitat issues discussed above, nor does it account for other environmental factors such as toxins, competitors or predators. If and when such information becomes available, this model could be modified to make use of it.

In conclusion, field surveys will discover that the species is not as widespread or abundant as predictions by this model suggest. The model predicts potentially available habitat. There are a variety of reasons why the habitat may not be utilized.

Definitions.

Home Range: the area regularly used for all life activities by an individual during the breeding season.

Dispersal Distance: the distance an individual will disperse to establish a new home range. In this model it is used to determine if Potential Colony Habitat will be utilized.

Day to Day Distance: the distance an individual is willing to travel on a daily or semi-daily basis to utilize a distant resource (Potential Day to Day Habitat). The distance used in the model is the home range radius. This is determined by calculating the radius of a circle with an area of one home range.

Core Habitat: a contiguous area of habitat of medium or high quality that has an area greater than two snowshoe hare home ranges in size. This habitat is in continuous use by the species. The species is successful enough in this habitat to produce offspring that may disperse from this area to the Colony Habitat and Other Habitat.

Potential Colony Habitat: a contiguous area of habitat of medium or high quality that has an area between one and two home ranges in size. It is not necessarily used continuously by the species. The distance from a core area will affect how often Potential Colony Habitat is utilized.

Colony Habitat: Potential Colony Habitat that is within the dispersal distance of the species. These areas receive their full original value unless they are further than three home range radii from a core area. These distant areas receive a value of low since there is a low probability that they will be utilized regularly.

Potential Day to Day Habitat: an area of high or medium quality habitat less than one home range, or habitat of low quality of any size. This piece of habitat alone is too small or of inadequate quality to be Core Habitat.

Day to Day Habitat: Potential Day to Day Habitat that is close enough to Core or Colony

Habitat can be utilized by individuals moving out from those areas on a day to day basis. The grid cell must be within Day to Day Distance of Core or Colony Habitat.

Other Habitat: contiguous areas of low value habitat larger than two home ranges in size, including small areas of high and medium quality habitat that may be imbedded in them, are included as usable habitat by the species. Such areas may act as “sinks” because long-term reproduction may not match mortality.

The table below indicates the specific distances and areas assumed by this model.

Distance variables:	Meters	Feet
Dispersal Distance	963	3,160
Day to Day Distance/ Home Range radius	161	527

Area variables:	Hectares	M ²	Acres	Ft ²
Home Range	8.09	80,940	20	871,200
Core Habitat	16.18	161,880	40	1,742,400

Application of the Model

A copy of the ARC/INFO AML can be found in Appendix 1. The steps carried out by the macro are as follows:

1. **Determine Core Habitat:** this is done by first converting all medium quality habitat to high quality habitat and removing all low value habitat. Then contiguous areas of habitat are grouped into regions. The area of each of the regions is determined. Those large enough (two home ranges) are maintained in the Core Habitat coverage. If no Core Habitat is identified then the model will indicate no suitable habitat in the study area.
2. **Identify Potential Colony Habitat:** using the coverage from Step 1, determine which

regions are one to two home ranges in size. These are Potential Colonies.

3. **Identify Potential Day Use Habitat:** using the coverage derived in Step 1, determine which areas qualify as Potential Day to Day Habitat.
4. **Calculate the Cost Grid:** since it is presumed to be more difficult for animals to travel through unsuitable habitat than suitable habitat we use a cost grid to limit travel based on habitat suitability. The cost to travel is one for high or medium quality habitat. This means that to travel 1 m through this habitat costs 1 m of Dispersal Distance. The cost to travel through low quality habitat is two and unsuitable habitat costs four. This means that to travel 1 m through unsuitable habitat costs the species 4 m of Dispersal Distance.
5. **Calculate the Cost Distance Grid:** a cost distance grid containing the minimum cost to travel from each grid cell to the closest Core Habitat is then calculated using the Cost Grid (Step 4) and the Core Habitat (Step 1).
6. **Identify Colony Habitat:** based on the Cost Distance Grid (Step 5), only Potential Colony Habitat within the Dispersal Distance of the species to Core Habitat is retained. Colonies are close enough if **any** cell in the Colony is within the dispersal distance from Core Habitat. The suitability of any Colony located further than three home range radii from a Core Habitat is changed to low since it is unlikely it will be utilized regularly.
7. **Create the Core + Colony Grid:** combine the Core Habitat (Step 1) and the Colony Habitat (Step 6) and calculate the cost to travel from any cell to Core or Colony Habitat. This is used to determine which Potential Day to Day Habitat could be utilized.
8. **Identify Day to Day Habitat:** grid cells of Day to Day Habitat are only accessible to the species if they are within one half of a home range radius from the edge of the nearest Core or Colony Habitat. Add these areas to the Core + Colony Grid (Step 7).
9. **Add Other Habitat:** large areas (two home ranges in size) of low value habitat, possibly with small areas of high and medium habitat imbedded in them may be utilized, although marginally. Add these areas back into the Core + Colony + Day to Day Grid (Step 8), if any exist, to create the final habitat suitability (HSI) map.
10. **Restore Values:** all areas that have been retained receive their original geometric mean value from the original geometric value grid with the exception of distant colonies. Distant colonies (colonies more than three home range radii distant) have their value reduced to low because of the low likelihood of utilization.

Problems with the Approach

Cost.

The cost to travel across low suitability and unsuitable habitat is not known. It is likely that it is quite different for different species. This model incorporates a reasonable guess for the cost of movement. A small bird will cross unsuitable habitat much more easily than a small mammal. To some extent differences in vagility between species is accounted for by different estimates of dispersal distances.

Dispersal distance.

The distance animals are willing to disperse from their nest or den site is not well understood. We have used distances from studies of the species or similar species when possible, otherwise first approximations are used. More research is urgently needed on wildlife dispersal.

Day to day distance.

The distance animals are willing to travel on a day to day basis to use distant resources has not been quantified for most species. This issue is less of a concern than dispersal distance since the possible distances are much more limited, especially with small mammals, reptiles, and amphibians. Home range size is assumed to be correlated with this coefficient.

SOURCES OF OTHER MODELS

Carrecker (1985) developed a snowshoe hare HSI model. This model considers the ability of winter habitat to meet the food and cover needs of the species as an indication of year-round habitat suitability. The variables in the model are the biomass of available browse and the average visual obstruction measurement of living and dead vegetation.

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APPENDIX 1: Snowshoe Hare Macro

```
/*      SNOWSHOE HARE
/* shamodel.aml - This macro creates an HSI coverage for the
/*      Snowshoe Hare.

/* Version: Arc/Info 6.1 (Unix), GRID-based model.

/* Authors: Irene Timossi, Sarah Miller, Wilde Legard,
/*          and Reginald H. Barrett
/*          Department of Forestry & Resource Management
/*          University of California, Berkeley

/* Revision: 2/10/95

/* -----

/* convert .ID to uppercase for info manipulations

&setvar .ID [translate %.ID%]

/* Start Grid

grid

/*

&type (1) Initializing Constants...

/* Homerange: the size of the species' homerange.

/* DayPay: The amount the species is willing to pay traveling on
/* a day-to-day basis. Used to determine the area utilized on a
/* day-to-day basis.

/* DispersePay: Distance traveled when dispersing. The amount
/* the animal is willing to pay when dispersing from a core area.

/* High: The value in the WHR grid which indicates high quality habitat.

/* Medium: The value in the WHR grid which indicates medium quality habitat.

/* Low: The value in the WHR grid which indicates low quality habitat.

/* None: The value in the WHR grid which indicates habitat of no value.

/* SpecCode: The WHR code for the species

/* AcreCalc: The number needed to convert square units
/*          (feet or meters) to acres.

&setvar SpecCode = M049

&if %.Measure% = Meters &then
&do
    &setvar Homerange    = 80940
    &setvar DayPay       = 161
    &setvar DispersePay   = 963
    &setvar AcreCalc      = 4047
```

```

&end
&else
  &if %Measure% = Feet &then
    &do
      &setvar Homerange    = 871200
      &setvar DayPay       = 527
      &setvar DispersePay  = 3160
      &setvar AcreCalc     = 43560
    &end
  &else
    &do
      &type Measurement type incorrect, check spelling.
      &type Only Meters and Feet are correct.
      &goto &BADEND
    &end

&setvar High      = 3
&setvar Medium    = 2
&setvar Low       = 1
&setvar None      = 0

/* The following global variables are declared in the menu:

/* .WHRgrid (WHR grid name): the name of the grid containing all
/* the WHR information.

/* .Bound (Boundary grid name): the grid containing only the
/* boundary of the coverage. All cells inside the boundary
/* have a value of 1. All cells outside the boundary must
/* have a value < 1.

/* .ID (Identifier): a 1 to 4 character code used to identify
/* the files produced by this program. You may prefer
/* to use an abbreviation of the species' common name
/* (e.g. use `fis1` for fisher).

/* .SizeOfCell (Cell size): the size (width) of the cells
/* used in the coverage grids. All grids used in the
/* analysis must have the same cell size.

/* .Measure: the units the coverage is measured in (feet or meters).

&type (2) Creating working grid of geometric means...

/* Create a Geometric Means grid (Geom) for the species by
/* copying these values from the WHR grid.

Geom = %.WHRgrid%.%SpecCode%_G

/*

&type (3) Changing %Medium% value cells to %High% value for Merge grid...

/* Create a grid (Merge) merging Medium and High
/* value cells from the Geometric mean grid (Geom),
/* while leaving the value of other cells (Low and None) unchanged.
/* Merge by changing the value of all medium cells to High.

Merge = con(Geom == %Medium%,%High%,Geom)

```

```
/*
```

```
&type (4) Converting Merge grid zones into a Region grid...
```

```
/* Convert the zones of the merge grid (Merge) into  
/* unique regions (Region). These will be used later  
/* to create core, colony, and day-to-day areas.
```

```
Region = regiongroup(Merge,#,EIGHT)
```

```
/*
```

```
&type (5) Calculating the area of Region grid zones...
```

```
/* Calculate the area of the zones (ZoneArea) on the region  
/* grid (Region).
```

```
ZoneArea = zonalarea(Region)
```

```
/*
```

```
&type (6) Creating a Core Area grid...
```

```
/* Extract areas from the zonal area grid (ZoneArea)  
/* suitable for core areas (Core). Core areas are defined  
/* as the Medium+High zones in the merge grid (Merge)  
/* with an area of at least two home ranges (%Homerange%).  
/* Set their value = 1.
```

```
if (Merge == %High% and ZoneArea >= %Homerange% * 2)  
    Core = 1  
endif
```

```
&if not [exists Core -vat] &then  
    &goto END
```

```
/*
```

```
&type (7) Creating a Colony grid...
```

```
/* Extract areas from the zonal area grid (zoneArea)  
/* possibly suitable for colonization (ColTemp).  
/* Colony areas are defined as Low or Medium+High zones  
/* in the Merge grid (Merge) with an area of between one  
/* and two home ranges (%Homerange%). Set their value = 1.
```

```
/* Then set all nodata values in the grid to zero (Colony).
```

```
docell  
    if (Merge == %High%)  
        if (ZoneArea > %Homerange% and ZoneArea < %Homerange% * 2)  
            ColTemp = 1  
        endif  
    endif  
end
```

```
Colony = con(isnull(ColTemp),0,ColTemp)
```

```
/*
```

```
&type (8) Creating a Day-to-Day Use grid...
```

```

/* Create a grid based on the values in the zonal
/* area grid (ZoneArea) and merge grid (Merge)
/* suitable for day-to-day use (DayToDay). Day-to-day use
/* areas are defined as Low if the area is less than two
/* homeranges in size or Medium+High zones in the
/* merge grid (Merge) with an area of less than one home
/* range (%Homerange%). Set their value = 1.

```

```

if ((Merge > %Low% and ZoneArea <= %Homerange%) or ~
    (Merge == %Low% and ZoneArea < %Homerange% * 2))
    DayToDay = 1
else
    DayToDay = 0
endif

```

```

/*

```

&type (9) Creating a Cost Grid based on habitat value...

```

/* Using the merge grid (Merge), create a cost grid (Cost)
/* based on the habitat-value. Cost represents the relative
/* resistance a species has to moving across different quality
/* habitat: Habitat-value Cost
/*          None          4
/*          Low           2
/*          Medium+High   1

```

```

if (Merge == %None%)
    Cost = 4
else if (Merge == %Low%)
    Cost = 2
else if (Merge == %High%)
    Cost = 1
endif

```

```

/*

```

&type (10) Calculating cost to travel from Core Areas...

```

/* Calculate the cost to travel the distance (CostDist)
/* from the nearest core area source (Core) using the cost
/* grid (Cost).
/*

```

```

CostDist = CostDistance(Core, Cost)

```

```

/*

```

&type (11) Calculating which Colony areas are Cost Effective...

```

/* If Colony Areas exist...
/* Find the areas in the Colony grid (Colony) that could
/* be colonized from the core areas:

/* Assign costs to all cells in the Colony areas (Colony)
/* from the Cost grid (CostDist). Zero surrounding NODATA areas.

/* Make each colony a separate zone (ZoneReg) using
/* the regiongroup command.

```

```

/* Use zonalmin to find the minimum cost to arrive at each
/* colony (ZoneMin).

/* Set all NODATA cells to zero in ZoneMin to produce
/* ColZer1.

/* To find out which of the potential colonies can be utilized,
/* determine which have a cost that is equal to or less than
/* DispersePay. If the cost to get to a colony is less than
/* or equal to DispersePay, keep it in grid Col.

/* Fill the null value areas in Col with zeros to create ColZer2

```

```

&if not [exists ColTemp -vat] &then
  &goto SkipColony

```

```

ColDist = con(Colony > 0, CostDist, 0)
ZoneReg = regiongroup(Colony, #, EIGHT)
ZoneMin = zonalmin(ZoneReg, ColDist)
ColZer1 = con(isnull(ZoneMin), 0, ZoneMin)

```

```

if (ColZer1 <= %DispersePay% and ColZer1 > 0)
  Col = Colony
else
  Col = Core
endif

```

```

ColZer2 = con(isnull(Col), 0, Col)

```

```

/*

```

```

&type (12) Creating Core + Colony grid...

```

```

/* If colonies exist...
/* Create a grid (ColCore) that combines the core
/* (Core) and colony (Colony) grids.
/* This grid will be used to analyze day-to-day use.

```

```

if (Colony == 1)
  ColCore = 1
else
  ColCore = Core
endif

```

```

&label SkipColony

```

```

&type (13) Calculate cost to travel from Core and Colony Areas...

```

```

/* If colonies exist...
/* Calculate the cost to travel the distance (CostDis2)
/* from the nearest core or colony area source (ColCore).
/* Otherwise just copy the CostDist grid to use for Day-to-Day
/* analysis.

```

```

&if not [exists ColTemp -vat] &then
  CostDis2 = CostDist
&else CostDis2 = CostDistance(ColCore, Cost)

```

/*

&type (14) Calculating which Day-to-Day areas are Cost Effective...

/* This step adds the utilized Day-to-Day cells to the
/* Core + Colony Area grid (ColZer2) to produce the
/* Day1 grid.

/* Use the Core + Colony Cost grid (CostDis2) to find out
/* what can actually be used day-to-day (any cell with
/* a cost of DayPay or less).

/* Retain any cell in the Day-to-Day grid (DayToDay) with
/* a cost less than or equal to DayPay and greater than zero.

/* If the Distance-Cost grid (CostDis2) = 0,
/* it is part of the Core or Colony Area and
/* should get its value from Core + Colony Area
/* grid (ColZer2).

&if [exists ColTemp -vat] &then

&do

if (CostDis2 <= %DayPay% and CostDis2 > 0)
Day1 = DayToDay

else

Day1 = ColZer2

endif

&end

&else

&do

if (CostDis2 <= %DayPay% and CostDis2 > 0)
Day1 = DayToDay

else

Day1 = Core

endif

&end

/*

&type (15) Finding Other Areas That May Be Utilized....

/* This step picks up any large low value areas and any small
/* medium or high value polygons that are imbedded
/* in them.

/* First find any areas that are not currently in the included
/* set (Day1Z) but are in the original geometric mean coverage (geom)
/* set Other to 1 where Day1Z = 0.

/* if Other is all nodata, create the All coverage from
/* the Day1Z coverage.

/* Split all other areas into separate regions (OthReg)

/* Calculate the area of the regions (OthArea).

/* Keep any region in OthArea with an area > 2 homeranges (Util).

/* Change any null values in Util to zeros (OthZero).

/* Add these areas to the Day1 coverage to create All

```

Day1Z = con(isnull(Day1),0,Day1)

if ((Day1Z < 1) and (Geom > 0))
  Other = 1
endif

&if not [exists Other - vat] &then
  All = Day1Z
&else
  &do
    OthReg = regiongroup(other,#,EIGHT)

    OthArea = zonalarea(OthReg)

    if (OthArea >= %Homerange% * 2)
      Util = 1
    else
      Util = 0
    endif

    OthZero = con(isnull(Util),0,Util)

    if (OthZero == 1)
      All = OthZero
    else
      All = Day1Z
    endif
  &end

/*
/*

&type (16) Creating a Value grid...

/* For any cell in All that has a value of 1, store the suitability
/* value from the Geometric mean grid (Geom) to the Value grid.

/* Other cells inside the boundary (%.Bound%) get a value of 0.

/*

if (All == 1)
  Value = Geom
else if (%.Bound% == 1)
  Value = 0
endif

/*

&type (17) Creating an HSI grid...

/* if Colonies exist....
/* For any cell that was part of a colony that is further than
/* 3 times the HR radius (DayPay) away from a core area, set the suitability
/* to Low. Distant colonies lose value because of their small size.
/* This step produces grid Collow.

/* Set all NODATA values in Collow to zero in ColZer3.

/* Find any day-to-day use areas (DayToDay) that are being

```

```

/* utilized (ColZer3). If they are further than four homeranges
/* from a core area (CostDist), they are utilized from a distant
/* colony and their value will be decreased to Low in Day2.

/* Then change nulls to zero in ValZero

/* Keep all data within the boundary; call this final grid HSI.

&if [exists ColTemp -vat] &then
  &do
    if (ColZer1 >= %DayPay% * 3)
      Collow = %Low%
    else
      Collow = Value
    endif

    ColZer3 = con(isnull(Collow),0,Collow)

    if ((CostDist > %DayPay% * 4) and (ColZer3 > 0) and ~
      (DayToDay == 1))
      Day2 = 1
    else
      Day2 = ColZer3
    endif
  &end
&else
  Day2 = Value

valzero = con(isnull(Day2),0,Day2)

if (%.Bound% == 1)
  %.ID%hsi = valzero
endif

/*

&type (18) Quitting from GRID and adding the acres field.....

/* Quit from GRID (Q), then run additem to add an acre item to
/* the HSI grid vat file (%ID%HSI.vat). Reindex on value when done.

Q
additem %.ID%hsi.vat %.ID%hsi.vat acres 10 10 i
indexitem %.ID%hsi.vat value

/*

&type (19) Calculating acres.....

/* Use INFO to calculate the acreage field: Multiply the number
/* of cells by the cell size squared and divide by the number of
/* square meters per acre (4047). Reindex on value when done.

&data arc info
arc
select %.ID%hsi.VAT
CALC ACRES = ( COUNT * %.SizeOfCell% * %.SizeOfCell% ) / %AcreCalc%
Q STOP

&END

```

indexitem %.ID%hsi.vat value

/*

&type (20) Killing all intermediate coverages before ending macro...

/* &goto OKEND

grid

kill Geom
kill Merge
kill Region
kill ZoneArea
kill Core
kill ColTemp
kill Colony
kill DayToDay
kill Cost
kill CostDist
kill ColDist
kill ZoneReg
kill ZoneMin
kill ColZer1
kill Col
kill ColZer2
kill ColCore
kill CostDis2
kill Day1
kill Day1Z
kill Other
kill OthReg
kill OthArea
kill Util
kill OthZero
kill All
kill Value
kill Collow
kill ColZer3
kill Day2
kill valzero

q

&goto OKEND

&label END
&type **
&type **
&type NO CORE AREAS EXIST, EXITING MACRO
&type **
&type **

kill Core
kill Region
kill ZoneArea
kill Merge
kill Geom

quit

&label OKEND
&label BADEND

&type ----- All done! -----

&return